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### ESTIMATES OF TEOSINTE INTROGRESSION IN ARCHAEOLOGICAL MAIZE

BY

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IN their monograph, "The Origin of Indian Corn and Its Relatives," Mangelsdorf and Reeves (1939) postulated that teosinte (*Euchlaena*) is the descendant of a natural hybrid between maize (*Zea*) and its wild relative *Tripsacum*, and that subsequent introgression from teosinte (i.e., ultimately from *Tripsacum*) has contributed significantly to the development of modern maize. The first of these postulates has not yet been proven, but evidence in support of the second has recently been found, not only in living races of maize, but also in archaeological remains of this economic plant. Studies of Wellhausen *et al.* (1952) indicate that the modern races of maize in Mexico have varying degrees of teosinte introgression, and that the most productive of these races were derived by combining different lines of introgression. In the prehistoric cobs from Bat Cave, which Mangelsdorf and Smith studied (1949), the earliest specimens appear to be "pure" maize, whereas later ones show evidence of contamination by teosinte. Further evidence of prehistoric introgression by teosinte comes from the upper

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strata of maize remains in nearby Tularosa Cave studied by Cutler (1952). At least three of the Tularosa Cave cobs illustrated by Cutler appear to be highly "Tripsacoid" (a term used first by Anderson and Erickson in 1941 to describe maize which tends, in some of its characteristics, to resemble *Tripsacum*). Also, some of the prehistoric cobs from the Hueco Mountain Caves in western Texas, as illustrated by Cosgrove (1947, Fig. 65), resemble those of Tripsacoid maize.

Archaeological material recently excavated from two caves in Arizona has yielded more abundant evidence on the role of teosinte (or *Tripsacum*) in the evolution of modern maize. This material, collected by the junior author, Mr. Lloyd Pierson, comes from Richards' Caves near Montezuma Castle and from the lower ruin in the Tonto National Monument in Arizona. It consists of the unusually large total of 3,342 well-preserved cobs, as well as numerous kernels, husks, shanks and tassel fragments. Its age is estimated at from 500 to 700 years.

Among the cobs are specimens which resemble closely those which occur in the  $F_2$  and backcross generations of maize-teosinte hybrids. In fact, it is possible to match many of these archaeological specimens, feature for feature, with modern cobs of segregates of maize-teosinte hybrids (Plates XXV and XXVI). These Tripsacoid cobs tend to be more indurated than the "pure" maize cobs in the same collection. This is regarded as highly significant, for one of the conspicuous differences between maize and its two relatives, teosinte and *Tripsacum*, is in the induration of the tissues, especially those of the rachis, cupule<sup>1</sup> and lower glumes. In both teosinte and *Tripsacum*, the caryopsis is enclosed in a hard, bony case

<sup>1</sup> The cupule or alveolus is a lignified structure thought to represent a prophyll adnate to the rachis, and to be borne on a reduced primary branch which bears a pair of pistillate spikelets (Nickerson, 1954).



composed of an internode of the rachis, a cupule and the lower glume. These structures become highly lignified as the fruit matures. Extensive experiments with maize-teosinte hybrids have demonstrated that the genes responsible for the lignification occur on many, if not all, of the chromosomes of teosinte. Indeed, in segregating generations of maize-teosinte hybrids, it is difficult to find individuals, even the most maize-like, which do not exhibit some degree of lignification of the rachis, cupule and lower glumes. Consequently, when in archaeological cobs strong induration (lignification) of these structures is encountered, teosinte introgression is at once suspected, especially when such induration is accompanied by solitary spikelets and two-ranked spikes, both teosinte characters, as is the case in some specimens. Unfortunately, the seeds of archaeological maize are not viable and it is not possible to obtain direct and final proof through breeding experiments. However, all of the facts presented here are consistent with the hypothesis that there has been such introgression.

Inasmuch as the hybridization of maize and *Tripsacum* has never been observed in nature and is, at best, rare, and since teosinte and maize do hybridize regularly in Guatemala and Mexico, we may, for the purposes of this discussion, assume that the prehistoric introgression represented by these archaeological specimens comes from teosinte rather than from *Tripsacum* and that this hybridization occurred in Mexico. We are left, however, with the possibility that maize has hybridized with local species of *Tripsacum* in the American Southwest and that the introgression involved is directly from *Tripsacum*, rather than indirectly through teosinte.

*Specific Gravity of Teosinte Derivatives and  
Archaeological Cobs*

Since the cobs of derivatives from maize-teosinte hy-



brids are more highly lignified and more dense than those of ordinary maize, it was hoped that a fairly direct estimate of teosinte introgression might be made by determining the specific gravity of the cobs. This proved for various reasons (for example, the presence or absence of pith) not to be the case. Nevertheless, it was found that in modern maize the specific gravity increases with known additions of teosinte germplasm; and that, among archaeological cobs, the Tripsacoid specimens have a significantly higher specific gravity, on the average, than the non-Tripsacoid ones.

Specific gravity was determined by liquid displacement, using a ten percent solution of alcohol as the liquid. The modern maize tested comprised single crosses of the inbred strains K155, L317, 701 and 38-11 with 4R-3 and with modified strains of 4R-3, in which two or three chromosomes of teosinte had been introduced through repeated backcrossing.

The data (Table I) indicate a significant positive relationship between degree of teosinte introgression and specific gravity. The more Tripsacoid cobs, in this case those known to have teosinte introgression, have a significantly higher specific gravity than the controls.

In archaeological maize, a parallel experiment was conducted by substituting estimates of the induration of the

TABLE I. Average specific gravity of cobs as compared to number of teosinte chromosomes in modern maize and degree of induration in archaeological maize.

Modern Cobs		Archaeological Cobs	
No. teosinte chromosomes	Av. sp. grav.	Grade of induration	Av. sp. grav.
0	.620	2	.658 ± .01
2	.680	3	.657 ± .01
3	.740	4	.690 ± .01 *

\* Grade-4 is significantly greater than either grades-2 or 3



cob for known teosinte introgression and correlating it to specific gravity. The archaeological material consisted of 217 cobs from Richards' Caves. Since induration is a subjectively determined character, all estimates were made by one person. Specific gravity determinations were made as with the modern specimens. Here again, the difference is significant, although the increase in specific gravity is not so great and is limited to the highest grade of induration. The curve expressing this relationship (Table I) would resemble that used by Anderson and Erickson (1941) to illustrate their hypothesis of antithetical dominance (a hypothesis suggesting that modifier complexes with sharp threshold effects control dominance of certain characters in wide hybrids).

*Tests for Lignification in Teosinte Derivatives  
and Archaeological Cobs*

Since cellulose is easily dissolved by concentrated sulphuric acid while lignified tissues are resistant, treatment with this acid is recognized as a specific test for lignin. It has been found that, when cobs of teosinte derivatives are so treated, they lose all of their tissues except the rind and cupules of the rachis and the lower glumes. When archaeological specimens are subjected to the same treatment, immersed for twenty-four hours in sulphuric acid, the Tripsacoid cobs remain almost intact, while the pure maize cobs disintegrate to a delicate framework of cupule margins (Plate XXVII).

It has already been mentioned that both modern and archaeological Tripsacoid cobs have a higher specific gravity than the non-Tripsacoid cobs. None of these facts in itself proves that the cobs in question are a product of maize-teosinte hybridization; but, together, they provide a reasonable presumption that such might be the case.



### *Estimates of Teosinte Introgression*

Since the archaeological Tripsacoid cobs, like modern maize-teosinte derivatives, have a higher specific gravity than non-Tripsacoid ones and are more resistant to erosion by sulphuric acid, it is assumed for the purposes of this study that induration of the tissues of the cob is a rough measure of teosinte introgression. Estimates of introgression were made with an arbitrary key of five grades. Grade-1 designates the pure maize extreme while grade-5 approaches a maize-teosinte  $F_1$  hybrid (Plate XXVIII). Although the degree of induration is the chief factor, single-pistillate spikelets distinguish the highest grade. Single-pistillate spikelets are characteristic of teosinte and are common in maize-teosinte hybrids, but absent in typical maize.

*Other Characters Studied.* Cob size has a particular interest for these studies, since previous work on archaeological maize indicates that an enlargement of the cob has been an outstanding feature of maize evolution (Mangelsdorf and Smith, 1949; Mangelsdorf, 1954). Both length and diameter of cob were measured. Other characters chosen for analysis were kernel-row number and fasciation. In smaller samples of the collection, the following internal characters were also studied: pilosity, cupule width, glume length and rachis diameter. Average estimates of teosinte introgression (average induration score) were determined for each morphological class by the use of key-sort cards. Correlation coefficients were then calculated and the data were plotted in curves. In the case of kernel-row number, however, the effects of teosinte introgression were studied independently for the fasciated and non-fasciated cobs. This distinction was made because fasciation is known to have an effect of its own on row-number.



The following procedures were observed in scoring the cob characters: 1) The number of rows of pistillate spikelets (kernel-row number) was counted in the central region of all intact and fragmentary cobs; 2) A fasciated cob was considered to be any cob which was obviously flat for at least one-quarter of its length. This flattening was generally observed at the tip of the cob where it is most frequent. Fasciation was not scored in the four-row class, although such cobs are at least superficially flat as a result of their bilateral nature; 3) Diameters were measured in the central region of all intact and fragmentary cobs. When cobs were fasciated, the average of maximum and minimum widths was used; 4) Length measurements were made only on obviously intact specimens (about one-third of the collection); 5) The internal characters (pilosity, cupule width, glume length and rachis diameter) were determined for a random sample of fourteen intact cobs from each grade of introgression. Pilosity was scored in six grades, the higher numbers indicating stronger pubescence. Cupule width was measured between the lateral wings or "rachis flaps" of the cupule.

#### RICHARDS' CAVE MAIZE

1,440 cobs were obtained from two of Richards' Caves. One of these caves was subdivided into five areas. Since the variability and averages of the data for these areas are similar, this collection has been treated as a whole (Table II).

*Kernel-row Number.* Teosinte introgression causes a decrease in row-number for all cobs from Richards' Caves, except non-fasciated ones that are above average in row-number (Table III). In these exceptional cobs, the initial relationship is reversed by an increase in introgression with row-numbers from twelve to sixteen,



TABLE II. Morphological characteristics of two populations of archaeological maize cobs

Richards' Caves											Tonto		
	Cave I	Cave II								Room 16	Area-A	Area-B	
		Room 1				Room 4		Room 6					
		Above floor		Cyst 1	Cyst 2								
No. cobs	150	880	160	30	20	187	1502*	343**	57				
Intact %	29	34	19	23	10	28	9	6	12				
Red %	9	4	7	17	10	7	5	7	—				
Fasciated %	—	16	13	13	40	11	23	26	28				
Unusual %	1	15	12	13	20	12	4	6	12				
(%) Teosinte Introgression	1	0.1	—	—	—	—	3	—	—				
	21	16	23	11	21	20	25	14	13				
	55	64	56	66	74	50	60	77	76				
	23	19	21	23	5	29	12	10	11				
	—	1	—	—	—	1	—	—	—				
(%) Kernel Rows	4	1	—	3	—	—	1	—	2				
	6	1	—	3	—	1	—	—	—				
	8	31	33	40	25	23	23	30	25				
	10	33	22	30	30	36	53	55	40				
	12	23	21	23	45	26	20	16	26				
	14	8	16	3	—	10	3	5	7				
	16	2	7	—	—	3	1	—	—				
	18	1	—	—	—	1	—	—	—				







and finally a decrease at eighteen rows (Fig. 1).

The general effect of introgression in reducing row-number appears to have a secondary effect in reducing the amount of fasciation. This is suggested by the fact that fasciation is significantly less frequent in Tripsacoid cobs (fourteen percent in grade-4) than in non-Tripsacoid ones (seventeen percent in grades-2 and 3). Apparently such an effect accentuates a tendency for fasciation to be concentrated in the high row-number, non-Tripsacoid cobs.

*Diameter.* Cob diameters in the Richards' Caves collection average 18.3 mm. Teosinte introgression has no significant effect on diameter in this population (Table III and Fig. 2).

*Length.* The length of 433 intact specimens from Richards' Caves averages 8.74 cm. The average in this case has little meaning, since, as is shown later, at least two factors are interacting to produce the variation in this collection. The longest and shortest cobs are the most Tripsacoid (Fig. 3 and Plate XXVIII). The fitness of the data to a parabolic curve is excellent (Table III).

*Internal Characters.* Teosinte introgression appears to affect the internal characters of the cobs from Richards' Caves as follows: it decreases pilosity, increases cupule width, and increases glume length. Rachis diameter and glume-rachis ratio appear not to be closely associated with introgression in the samples studied (Table IV).

*Kernels.* A majority of the 140 mature kernels from Richards' Caves have a yellow, flinty endosperm; the remainder are floury. A few of both types have a red pericarp. The dimensions (Table V) show that the grains are quite uniform in size and probably are too large to pop. Almost half of the grains are definitely immature.



TABLE III. Test for significance of correlations between Teosinte introgression and kernel rows, diameter and length for cobs from Richards' Caves.

Character	Correlation	d.f.	Probability
Kernel rows *	-0.851 <sup>1</sup>	5	<.05
Diameter	0.075 <sup>1</sup>	6	>.05
Length	0.859 <sup>2</sup>	14	<.01

\* Fasciated cobs

<sup>1</sup> Linear

<sup>2</sup> Parabolic curvilinear

TABLE IV. Certain internal characters for samples of 14 intact cobs from various levels of teosinte introgression in Richards' Caves maize.

Introgression <sup>1</sup>	Pilosity <sup>2</sup>	Cupule width(mm.)	Glume Length (mm.)	Rachis Diameter(mm.)	G/R Ratio
2	5.0	7.0	3.0	10	.30
3	4.3	7.3	4.0	11	.36
4 (long) <sup>3</sup>	2.3	9.7	4.2	15	.28
4 (short) <sup>4</sup>	1.8	9.1	4.2	10	.42

<sup>1</sup> Grade-5 is most tripsacoid

<sup>2</sup> Grade-5 shows strongest pubescence

<sup>3</sup> Av. length 13.5 cm.

<sup>4</sup> Av. length 4.0 cm.

TABLE V. Frequency and average dimensions (mm.) of various types of caryopses from Richards' Caves.

Type	Frequency	Length	Width	Thickness
Flour - Y	14	8.0	8.5	6.1
Flour - P	4	7.5	8.5	5.5
Flint - Y	121	7.5	8.5	5.7
Flint - P	1	8.0	9.0	5.8
Immature	100	—	—	—

Y - yellow endosperm, colorless pericarp

P - red pericarp



This suggests that some of the ears were consumed in the green or roasting stage.

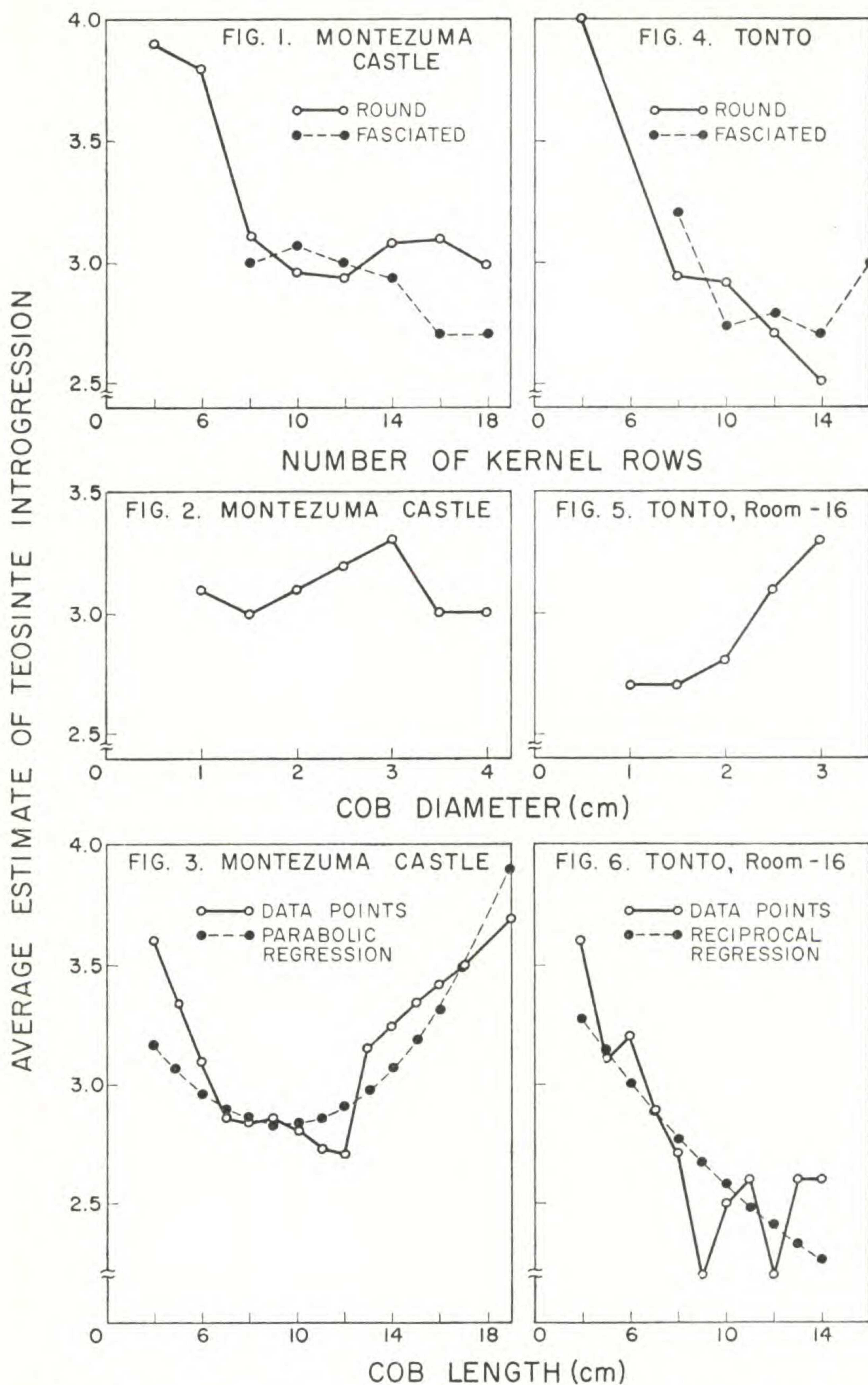
### TONTO MAIZE

This lot of 1902 cobs was obtained from three areas. The majority (seventy-nine percent), however, came from a single location (Room 16). The material may therefore be considered as a unit (Table II). Analysis was restricted to a representative sample of 500 cobs (twenty-six percent of the total), which included all intact specimens (162 cobs). The cobs are relatively uniform and many are broken. Increased breakage in the Tonto cobs (ninety-one percent as compared to seventy percent for Richards' Caves) may be attributed to a significantly lower level of teosinte introgression (Table VI).

*Kernel-row Number.* Kernel-row number in non-fasciated cobs decreases significantly with increasing levels of introgression. In contrast to this, the row-number of fasciated cobs appears to be independent of introgression, or at least the relationship is complicated by other factors (Table 7 and Fig. 4). Fasciation is more common at Tonto (twenty-five percent as compared to fourteen percent for Richards' Caves) and is associated with pure maize (twenty-eight percent fasciation at grade-2; twenty-five percent at grade-3; and eleven percent at grade-4). At the average row-number of ten, fasciation prevails in twenty-three percent of the cobs (a frequency twice as high as in the ten-rowed cobs from Richards' Caves, and many times that which is characteristic of most modern races).

*Diameter.* Tonto cobs are slender, averaging only 16.5 mm. in diameter (2 mm. less than in Richards' Caves). Teosinte introgression increases the diameter of these cobs (Table VII and Fig. 5).





FIGURES 1-6. Curves showing the relationships between estimates of teosinte introgression and various cob characters for Richards' Caves [indicated above as Montezuma Castle] and Tonto maize.



*Length.* The length of intact cobs from Tonto averages 8.3 cm. (0.5 cm. less than in cobs from Richards' Caves). Teosinte introgression causes a general decrease in cob length. This relationship is best illustrated by a reciprocal regression curve, rather than by a straight line (Table VII and Fig. 6).

*Kernels.* The 511 kernels recovered from Tonto are largely of a yellow, flinty type; the remainder being floury. A few of both types have red or cherry-colored pericarps (in solid and variegated patterns). Forty-three flinty grains have their embryos and pericarps removed, perhaps in preparation for grinding. All kernels are mature, uniform, and too large for good popping (Table VIII).

### *Unusual Specimens*

Cobs with unusual morphological characteristics were found in both collections. These distinguishing features include: long glumes; "Siamese" twinning (duplication of rachis followed by incomplete divergence); lateral fusion of cupules (15 laterally-fused cupules found in one spiral); solitary cupules terminal to the cob and free from adjoining rachis tissue; close similarity to maize-teosinte hybrids; unusual extremes in size, fasciation, etc.

*Prehistoric Tunicate Maize.* One of the few archaeological specimens known to duplicate the extreme form of modern tunicate maize occurs among the long-glumed cobs (Plate XXIX). A similar specimen has previously been reported by Cutler (1944) from the Betatakin Pueblo Ruin near the San Juan River in Arizona. Our tunicate specimen, as well as five other long-glumed cobs from Richards' Caves, are Tripsacoid (Table IX). The actual level of introgression in these cobs may be partially masked by the tunicate condition. Thus, their esti-



TABLE VI. Comparison between certain morphological features of Richards' Caves and Tonto maize cobs.

	Richards' Caves	Tonto	t-value	d.f.	Probability
Teosinte Int.	3.03	2.89	5.02	1901	<.01
Kernel Rows	10.36	10.04	2.76	1890	<.01
Diameter (mm.)	18.27	16.46	7.66	1917	<.01
Length (cm.)	8.74	8.26	1.52	593	>.05

TABLE VII. Test for significance of correlations between Teosinte introgression and kernel rows, diameter and length for Tonto cobs.

Character	Correlation	d.f.	Probability
Kernel rows			
(a) fasciated cobs	0.296 <sup>1</sup>	4	>.05
(b) round cobs	-0.951 <sup>1</sup>	4	<.01
Diameter	0.984 <sup>1</sup>	4	<.01
Length	0.725 <sup>1</sup>	10	<.01
Length	0.978 <sup>2</sup>	10	<.01

<sup>1</sup> Linear

<sup>2</sup> Reciprocal curvilinear

TABLE VIII. Frequency and average dimensions (mm.) of various types of caryopses from Tonto.

Type	Frequency	Length	Width	Thickness
Flour - Y	13	8.0	9.0	5.8
Flour - P	9	8.3	8.0	6.2
Flint - Y	374	8.0	8.0	4.8
Flint - P	72	7.5	8.0	5.1
Fragments	43			

Y - yellow endosperm, colorless pericarp

P - red or cherry (solid or variegated) pericarp



mated introgression score is probably lower (closer to pure maize) than is really the case. Such a possibility is suggested by comparisons of cupule width and pilosity between the tunicate and non-tunicate cobs (Tables IV and IX).

TABLE IX. Certain internal characters of tunicate-like cobs from Richards' Caves maize.

Cob No.	Introgression <sup>1</sup>	Pilosity <sup>2</sup>	Cupule Width(mm.)	Glume Length(mm.)	Rachis Diameter(mm.)	G/R Ratio
104	2	3	8.0	9	12	.75
62	2	3	10.0	7	17	.41
59	2	1	8.0	6	9	.66
598	2	1	9.0	5	11	.45
319	3	0	12.0	5	12	.42
798	2	1	7.0	5	9	.55

<sup>1</sup> Grade-5 is most tripsacoid

<sup>2</sup> Grade-5 shows strongest pubescence

### *Other Maize Remains*

*Richards' Caves.* The twenty-two tassel fragments in this collection are not particularly significant in relation to teosinte introgression. The husk fragments (seventy-seven in number) are characteristic of Tripsacoid maize in that they are hispidulous (beset with minute epidermal bristles). Tripsacoid characteristics of fourteen culm fragments include a prominent, lignified rind and numerous vascular bundles. The shanks (thirty-six in number) are similar to the culm fragments in lignification. They are also rather uniform in length (5 to 7 cm.), although there is considerable variation in diameter (0.5 to 3.0 cm.) and in their having from six to ten nodes. This lot also yielded seven boluses, consisting of wadded and sometimes chewed grass leaves, probably from maize or its relatives.



*Tonto*. There are thirty tassel fragments, twenty-seven husks and fifty-two shanks from this site. These are not morphologically unusual or different from those of modern maize. There are also two depauperate culms bearing small ears near the basal end; three carbonized cobs; and twenty-two boluses which are similar in character to those from Richards' Caves.

## DISCUSSION

The earliest reports of natural hybrids between maize and teosinte date back to the "*Zea canina*" of Watson (1891). Harshberger later reported (1896) the findings of Professor J. C. Segura, which indicated that these plants were maize-teosinte hybrids. This has been confirmed by examining the Watson specimens preserved in the Gray Herbarium. Today, natural hybridization between teosinte and maize occurs frequently in Guatemala and Mexico. Although Randolph (1955) considers such hybridizations to be rare, his conclusion is inconsistent with the literature, as well as with his own observations. For example, he reports (1955, p. 45) finding 45  $F_1$  and 3  $F_2$  teosinte-maize hybrids near the villages of Nojoyá and San Antonio Huixta in northwestern Guatemala. Also from this region, where teosinte is the dominant plant over thousands of acres, Kempton and Popenoe (1937, p. 211) found in a collection of seed "several spikes of unmistakable hybrids." These authors report further that the farmers in the Jutiapa region of Guatemala "appreciated that teosinte hybridizes with corn and most informants lose no time in explaining that this plant will become corn in three generations if seed from the hybrid plant is grown." From Santa Ana Huixta, Guatemala, spikes of  $F_1$  hybrids of maize and teosinte were present in teosinte collected by F. W. McBryde for the Harvard Botanical Museum (Mangelsdorf, unpub.). Such hybrids



are more frequent in the Chalco region near Mexico City, where Mangelsdorf (1952) found that slightly more than one percent of the "maize" plants in a cultivated field were actually  $F_1$  hybrids of maize and teosinte. Even the small colony of perennial teosinte in Jalisco, Mexico, is reported by Collins (1921) to have contained a plant resembling an  $F_2$  segregate of a maize-teosinte hybrid. Weatherwax (1935) mentions that, although maize-teosinte hybrids are continually coming into existence, the parent species do not blend because the intermediate forms have no survival value. Nevertheless, reciprocal introgression does occur between these species to the extent that it does not become deleterious. The result is the development of new races of teosinte and new races of maize. For example, the teosintes of Mexico usually have the same plant characters as the race of maize with which they commonly grow, while the maize from the same region shows evidence of teosinte introgression (Collins, 1921, and others). In this connection, all of the more productive races of maize in Mexico show evidence of teosinte introgression, some of which has come directly from outcrossing to teosinte (Wellhausen *et al.*, 1952). This beneficial effect of teosinte introgression is recognized by certain natives in western Mexico, as is evident from their practice of interplanting *maizillo* (almost certainly teosinte) and maize for the purpose of improving the latter (Lumholtz, 1902).

Randolph also questions whether these hybridizations have led to any significant amount of teosinte introgression in modern maize. It may be that local introgression has little influence in any one generation, but occurring over the centuries, it is almost certain to have some effect. Furthermore, Randolph's view is inconsistent with the archaeological evidence. The oldest archaeological cobs from Mexico and southwestern United States have soft,



leathery glumes, while in the more recent levels in these areas there is a sudden influx of *Tripsacoid* cobs. Some of these closely resemble derivatives from maize-teosinte hybrids in having highly lignified, crateriform lower glumes which diverge at right angles from a highly lignified rachis, distichous arrangement of spikelets, and occasional single spikelets resulting from a partial or complete reduction of the second, or pedicellate spikelet (Mangelsdorf and Lister, 1956). This sudden appearance in maize of as many teosinte characters as one can get from hybrids of maize and teosinte cannot be explained as resulting from parallel or random mutation as Randolph claimed. In addition, the evidence of prehistoric maize-teosinte heterosis, as revealed by the present study, suggests how teosinte germplasm has been maintained during recent evolution in maize.

Conclusions from the extensive experimental work which has been done on the relation of teosinte to modern maize have a direct bearing on interpreting the archaeological material described in this paper. The nature of teosinte germplasm has been described by Mangelsdorf and Reeves (1939) as consisting of multiple factor segments distributed on several maize-like chromosomes, these segments having similar effects on the morphological characters which distinguish the ears of these species. It is also known that the various teosinte varieties themselves have both qualitative and quantitative differences in germplasm affecting the teosinte characters (Rogers, 1950). This teosinte germplasm may be involved in heterosis, for its effects on maize may be beneficial when heterozygous and deleterious when homozygous (Mangelsdorf, 1952). Furthermore, maize inbreds in Texas vary in their capacity to be improved by teosinte introgression, as demonstrated by Reeves (1950). This variability also occurs in Mexican maize, since races grown at



low altitudes generally benefit from teosinte introgression (as indicated by chromosome knob number), while those grown at high altitudes suffer from introgression (Wellhausen and Prywer, 1954).

In the archaeological material, the strongest correlations between the characters studied have been between teosinte introgression and cob length; but the two curves expressing this relationship in the 'Tonto and Richards' Caves material are different, at least in regard to the extension of the curve. For example, the relationship between cob length and introgression at Richards' Caves is described as parabolic curvilinear, while at Tonto it is reciprocal curvilinear. A parabolic curvilinear correlation suggests that more than one casual factor is involved; and, in light of the evidence from modern material, it is explicable in this case in terms of teosinte homozygosity and heterozygosity. That is, the short Tripsacoid cobs represent a product of homozygosity for teosinte germplasm, while the long Tripsacoid cobs are a result of maize-teosinte heterosis. The reciprocal curvilinear correlation between these factors in Tonto maize appears to correspond to the left half of the parabolic curve for Richards' Caves maize. After considering the experimental data on modern maize, the lack of this apparent heterosis in Tonto cobs might be accounted for in one or more of several ways, such as: 1) introgression from a different type of teosinte germplasm; 2) different residual inheritance from maize; and 3) a breeding restriction on the spread of introgression. The last possibility is suggested because of the significantly lower average level of introgression at Tonto.

This "heterotic effect" on length of the cobs from Richards' Caves appears to be reflected in the kernel-row numbers of non-fasciated cobs. In this case, the heterotic stimulation (right side of the parabolic curve) is not as



great and actually declines again in the highest row number class. These results are again explicable in terms of modern maize. Normally heterotic vigor tends to increase row numbers within certain limits. In the archaeological material, the highest row number class probably tends to be beyond the range of introgression. As might be expected, the lack of heterosis in length of Tonto cobs is repeated in regard to kernel-row number. That is, introgression has only a general effect in reducing row numbers.

A third factor distinguishing these collections lies in the relationship between cob diameter and introgression. Although these characters are independent at Richards' Caves, diameters increase significantly with introgression in Tonto cobs. Thus, the more Tripsacoid Tonto cobs have greater diameters, lower row numbers and shorter ears. The first two of these characters suggest introgression from the indurated Northern Flints, but the third one seems to rule this out since these flints have long ears.

*Fasciation and Row Number.* Introgression tends to eliminate fasciation, or flattening of the rachis, by causing a slight reduction in row number. Nevertheless, in comparison to modern maize, fasciation is extremely frequent in the lower row numbers. In modern maize, fasciation is usually confined to row numbers well above the range of this prehistoric material. These facts suggest that teosinte introgression may so modify the expression of genes for fasciation that increases in row number are produced without the association of a flattened rachis.

#### SUMMARY

1. Among archaeological cobs from Tonto and Richards' Caves in Arizona, there are many specimens which resemble, in appearance, those which occur in the  $F_2$  and backcross generations of maize-teosinte hybrids.



2. Such cobs, because of their greater lignification, also resemble modern teosinte-contaminated maize in having a higher specific gravity and greater resistance to the action of sulphuric acid.

3. On the basis of induration or lignification of the cob, estimates were made of the amount of teosinte introgression in the archaeological specimens and correlations were calculated between these estimates and various morphological features of the cob.

4. The most significant correlations found were between teosinte introgression and cob length, but the curves expressing this relationship in the Tonto and Richards' Caves material are different.

The Richards' Caves material shows that teosinte introgression is associated with both longer and shorter cobs, indicating that maize-teosinte heterosis produces beneficial effects, while the homozygous expression of teosinte germplasm has detrimental effects. There is also an indication of the same sort of effects on kernel-row number, although no relation was found between diameter and introgression.

In the Tonto material there is no evidence of heterosis in regard to length and row number, although diameters do increase with introgression.

The different effects of introgression within and between these archaeological collections emphasize the complexity of the effects of teosinte introgression—sometimes beneficial, at other times detrimental or ineffective.

5. This material also has a bearing on the problem of the role of fasciation and teosinte introgression in the evolution of extreme polystichy of the ear. The results indicate that introgression modifies the expression of



genes for fasciation in such a way that they increase row numbers without causing a flattening of the rachis.

6. One of the few archaeological cobs known which duplicates the extreme form of modern tunicate maize, was found in these collections.

#### LITERATURE CITED

- Anderson, Edgar and R. O. Erickson, 1941. Antithetical dominance in North American maize. *Proc. Nat. Acad. Sci.* 27: 436-440.
- Collins, G. N., 1921. Teosinte in Mexico. *Jour. Hered.* 12: 338-350.
- Cosgrove, C. B., 1947. Caves of the upper Gila and Hueco areas in New Mexico and Texas. *Papers of the Peabody Museum, Harvard Univ.* 24: 1-181.
- Cutler, H. C., 1944. Medicine men and the preservation of a relict gene in maize. *Jour. Hered.* 35: 291-294.
- , 1952. A preliminary survey of plant remains of Tularosa Cave. *Fieldiana: Anthropology (Chicago Nat. Hist. Mus.)* 40: 461-479.
- Harshberger, J. W., 1896. Fertile crosses of teosinte and maize. *Garden and Forest* 9: 522-523.
- Kempton, J. H. and W. Popenoe, 1937. Teosinte in Guatemala. *Carnegie Inst. Wash. Publ.* 483: 199-218.
- Lumholtz, C., 1902. *Unknown Mexico I.* Charles Scribner's Sons, New York.
- Mangelsdorf, P. C., 1952. Hybridization in the evolution of maize. *in Heterosis*, Iowa State College Press.
- , 1954. New evidence on the origin and ancestry of maize. *Amer. Antiquity* 19: 409-410.
- and R. G. Reeves, 1939. The origin of Indian corn and its relatives. *Texas Agric. Exper. Sta. Bull.* 574.
- and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. *Bot. Mus. Leaflets, Harvard Univ.* 13: 213-247.
- and R. H. Lister, 1956. *Bot. Mus. Leaflets, Harvard Univ.* (in press).



- Nickerson, N. H., 1954. Morphological analysis of the maize ear. Amer. Jour. Bot. 41: 87-92.
- Randolph, L. F., 1955. Cytogenetic aspects of the origin and evolutionary history of corn. *in* Corn and Corn Improvement (Vol. V of Agronomy). Academic Press Inc., New York.
- Reeves, R. G., 1950. The use of teosinte in the improvement of corn inbreds. Agron. Jour. 42: 248-251.
- Rogers, J. S., 1950. The inheritance of inflorescence characters in maize-teosinte hybrids. Genetics 35: 541-558.
- Watson, S., 1891. Contributions to American botany. III. Upon a wild species of *Zea* from Mexico. Proc. Amer. Acad. Arts and Sci. 26: 124-163.
- Wellhausen, E. M., *et al.*, 1952. Races of maize in Mexico. Bussey Institution of Harvard Univ.
- and C. Prywer, 1954. Relationship between chromosome knob number and yield in corn. Agron. Jour. 46: 507-511.